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## SHORTER ARTICLES AND DISCUSSION

### MR. MULLER ON THE CONSTANCY OF MENDELIAN FACTORS

IN discussing the selection experiments of Phillips and myself with hooded rats,<sup>1</sup> Mr. Muller<sup>2</sup> accepts the explanation of "modifying factors" which we offered to account for certain peculiar results obtained, but rejects the idea which we also suggested, that the chief genetic factor concerned may be undergoing quantitative variation. He rejects it on the ground that this explanation is not "in harmony with the results of Johannsen and other investigators." The work of Johannsen with seed-size in beans and the work of others with *Drosophila* is cited in support of this statement.

It is difficult to understand how the experiments of Johannsen have any direct bearing on the case since no single Mendelizing unit-factor was demonstrated in that connection; but in the hooded pattern of rats a Mendelizing unit-factor is unmistakably present and it is the quantitative variation of this which is under discussion, not the presence of many or few additional factors, concerning which Muller adopts our explanation. Appeal to the work of Johannsen with bean-size to show that our conclusions concerning color pattern in rats are incorrect is illogical because the cases are not parallel. The citation by Muller of the work on rabbit-size by MacDowell and myself<sup>3</sup> is equally non-germane, because no demonstrable Mendelizing unit-factor is involved in that case either. He might with propriety cite the bean work as bearing on the interpretation of the inheritance of body size in animals, or *vice versa*, since both involve blending inheritance. But neither of these cases has any direct bearing on the question of unit-character constancy, since in neither case has a unit-character, either constant or inconstant, been shown to exist.

The citation of work with *Drosophila* is more to the point, since the "mutations" of *Drosophila* Mendelize. But is it certain that they do not vary? Muller admits that they do *occasionally* vary, stating that "in one case (possibly in two or three cases)

<sup>1</sup> Castle and Phillips, "Piebald Rats and Selection," Publ. No. 195, Carnegie Institution of Washington.

<sup>2</sup> AMER. NAT., Vol. 48, p. 567.

<sup>3</sup> Publ. No. 196, Carnegie Institution of Washington.

a locus has mutated three times, each time in a different way." He does not think that smaller changes than these have occurred, since "much smaller could easily have been detected." From this statement I infer that the opinion rests on casual inspection rather than measurement, for which reason I do not attach much importance to it. The hooded pattern of rats was not supposed to vary quantitatively until its quantitative study was undertaken. Two types of hooded rats were recognized, one more extensively pigmented than the other, and these were supposed to be discontinuous like the several "mutations of a locus" in *Drosophila*. Quantitative study has completely dispelled this idea as regards the hooded pattern of rats, and I have no doubt the same would be true of *Drosophila*. How easy it is to be sure of a thing which has not yet been investigated, so sure that investigation of it is considered a waste of time. Muller is confident that such variation as occurs in *Drosophila* "can not even remotely be compared to fluctuating variability," and he generalizes thus:

"In no known case do the variations of a gene among, let us say, several thousand immediate descendants of the individual possessing it, form a probability curve."

The use of the word "gene" in this sweeping statement safeguards the author, since no one, so far as I know, claims ever to have seen a "gene" or to have measured it. How could the "variations of a gene" be expected to "form a probability curve" if the gene is not measurable? But if the author will allow the substitution of *visible character* for "gene" in his challenge, I will gladly accept it and I will add this generalization for his consideration—*No one has by actual observation and measurement shown the existence of any visible character in any animal which is not quantitatively variable.*

As regards the mutations of *Drosophila* which Muller is confident (apparently without having studied the matter himself) do not vary so as to form a probability curve, I had sufficient curiosity some months ago to suggest a quantitative study by one of my pupils, Mr. D. H. Wenrich. Mr. Wenrich studied the wing-length of flies from a culture kindly supplied me by Professor Morgan under the name "vestigial." In advance of a more detailed publication, Mr. Wenrich kindly permits me to state the following facts. The wing length measured in ocular micrometer units was found to vary as follows:

Classes .....	25-29	30-34	35-39	40-44	45-49
Frequencies .....	6	34	67	43	13
Classes .....	50-54	55-59	60-64	65-69	
Frequencies .....	1	1	0	1	

The wing-length manifestly varies so as to form a pretty good probability curve; what the "gene" is doing, I do not undertake to say.

It is, of course, conceivable that the variation here observed in actual wing length might be due to variation in general body size, larger flies having longer wings. To determine this point measurements of tibia-length were made on the same flies, and in the case of each individual the ratio was computed between wing-length and tibia-length. These ratios are distributed as follows:

Ratios .....	.70-.79	.80-.89	.90-.99	1.00-1.09	1.10-1.19	1.20-1.29
Frequencies	2	7	26	49	47	23
Ratios .....	1.30-1.39	1.40-1.49	1.50-1.59	1.60-1.69	1.70-1.79	
Frequencies	7	3	0	0	2	

It is evident that there is no constant relation between wing-length and tibia-length, and so between wing-length and general size, with which tibia-length is closely correlated. Again we obtain a good probability curve. Does the "gene" vary or are we dealing also with additional modifying "genes"? We are confronted here with the same problem as in the case of the rats.

But it is possible to assume that the considerable variation shown by vestigial wings in *Drosophila* is purely somatic, "phenotypic," not due to genetic causes, and so would not show any effects if subjected to selection. So it was thought in the case of the plus and minus variations in the hooded pattern of rats, *before the experiment was made*, but experiment has shown, even to Mr. Muller's satisfaction, that the variations are in part due to genetic causes and that selection slowly and surely changes the range of variability. Is it safe to assume the contrary for *Drosophila* in the absence of all experiment?

Mr. Wenrich has also studied the wing-length of "extracted" vestigial flies obtained in the second generation from a cross between pure vestigials and normal flies, and he finds that the variability is regularly increased as compared with that of the uncrossed vestigial race. This again is parallel with what occurs when hooded rats are crossed with wild or with Irish rats, and indicates that similar causes are at work in the two cases. Such

cases present to the genotype theory the following dilemma. Either *one* gene is concerned in the case or many genes. If one only is concerned, it is variable. If many genes are concerned, they are so numerous (whether or not constant) that they present to the observer of the visible character affected a continuous variation series, one capable of indefinite displacement up or down the quantitative scale. The supposed distinction between continuous and discontinuous variation then vanishes. Selection in that case meets with no "*fixed limit*" beyond which it cannot go.

Mr. Muller is seriously disturbed (p. 573) because we are willing to consider it possible that the "factor for hooded" may be contaminated by "its allelomorph (the factor for self)" while associated with it in the zygote represented by the  $F_1$  rats. (The evidence of modification is unmistakable, however one attempts to explain it.) He says this is "violating one of the most fundamental principles of genetics—the non-mixing of factors—in order to support a violation of another fundamental principle—the constancy of factors." Now, when, I should like to inquire, did these principles become "fundamental"; by whom were they established and on what evidence do they rest? I should suppose that Bateson, president of the British Association, might be considered fairly well posted on the "principles of genetics," but neither in his earliest papers nor in his latest do we find any mention of these sacred principles. In his recent presidential address<sup>4</sup> he frankly states his belief that segregation is often imperfect and that "fractionation" of factors frequently occurs as a result of crossing.

We shall look in vain, I think, for those "principles" outside of the "*Exakten Erblchkeitslehre*" (or its imitations), and when we inquire as to the experimental basis of the principles in question we are met with the satisfied reply, "*Johannsen's beans*." What a slender basis and what an absurd one from which to derive the "fundamental principle" that Mendelian factors are constant! Yet to date this case, which admittedly involves no clear Mendelian factor, is the only evidence worth mentioning in favor of the constancy of *Mendelian factors*! Do biologists take themselves seriously when they reason thus? Certainly no one else will long take them seriously.

Finally, I may be permitted to correct two misapprehensions

<sup>4</sup> *Science*, August 28, 1914.

into which Muller in common with the Hagedoorns<sup>5</sup> has fallen, viz., (1) that individual pedigrees were not recorded in the course of our selection experiments and (2) that no considerable amount of inbreeding occurred in our work.

It has been our invariable practise, upon recording the birth of an animal and its grade, to record on the same line of the ledger the record number of its mother and father. This enables one in any particular case to trace back the pedigree to the very beginning of our experiments. We have spent much time writing out and studying individual pedigrees, but without discovering any evidence of pure or prepotent lines or individuals, except in a single case, that of our "mutant" series, the origin and complete history of which we have described in detail. The pedigrees, however, of our rats are on record available for study at any time; their full publication would be a quite impossible undertaking.

That extensive and intensive inbreeding has occurred in our experiments will be obvious when I state that all our animals were descended from a very small initial stock, less than a dozen individuals, that from the beginning we have made the most extreme selections possible, mating like with like, never hesitating to mate brother with sister, and putting aside for strict brother-sister matings any litter of young which seemed especially promising. I may say that in no single case (except that of the "mutant" series) have these "special" pens given us advancement obviously greater or less than that of the general selection series of which they formed a part. Nevertheless, we are still continuing to follow them up and will later publish a detailed account of them. Finally I would call attention to pp. 20 and 21 with Tables 48-49 of our full publication, in which are described the hooded offspring of a single selected hooded and a single wild rat. The hooded and the wild rat produced several young resembling the latter, that is, not hooded; these were mated *inter se*, brother with sister. Among the grandchildren ( $F_2$ ) occurred the usual 25 per cent. of recessives, hooded. Two males were selected from these and mated with females of as nearly the same grade as were available. This process was repeated through seven generations in succession. Seven times animals of like grade were mated together, brother

<sup>5</sup> *Zeit. f. ind. Abst. u. Vererbungslehre*, 11, p. 145. See also my reply in the same journal, 12, p.

with sister when possible, less often brother with half-sister, rarely cousin with cousin. In this way were obtained 804 young from rigidly selected, closely inbred descendants of a single pair of rats, the series extending into generation  $F_8$ . We have shown (*l. c.*, p. 21) that the progress of selection within this inbred family follows a remarkably close parallel, generation by generation, to the progress of selection in our plus series as a whole. Muller's anticipation that a different result would follow close inbreeding is not justified by our observations.

In discussing this experiment (p. 21) we have italicized the statement that (so far as the hooded character is concerned) *the entire series is derived from a single hooded individual!* When the Hagedoorns made the statement that our stock had not been sufficiently inbred, they had apparently not seen our full publication and so had no means of knowing to what extent it had been inbred, but Muller, with our full publication before him, apparently repeats the statement without taking the trouble to verify it.

W. E. CASTLE

BUSSEY INSTITUTION,  
October 23, 1914

### NO CROSSING OVER IN THE FEMALE OF THE SILKWORM MOTH

IN a recent review<sup>1</sup> of a paper by Y. Tanaka<sup>2</sup> on linkage in the silkworm moth, I pointed out that some of his data suggested that crossing over was occurring in only one sex. While the data were not sufficient to establish this conclusion, there was at this time another paper by the same author<sup>3</sup> which I had not seen. In this paper are presented data which clear up the matter.

Tanaka has now made back-cross tests of both sexes. That crossing over does occur in the males was shown by the mating  $\text{sysy}\text{♀} \times \text{SYsy}\text{♂}$ , which gave a total of 865 cross-overs among 2,907 offspring. The cross  $\text{sysy}\text{♀} \times \text{SysY}\text{♂}$  gave 151/488 as the proportion of cross-overs. But when females were tested,  $\text{SYsy}\text{♀} \times \text{sysy}\text{♂}$  gave no cross-overs in 1,183 offspring. Tanaka refers to another paper, apparently in press, in which he has shown the same relations (*i. e.*, crossing over in males, none in

<sup>1</sup> AMER. NAT., XLVIII, 1914.

<sup>2</sup> Jour. Coll. Agr. Tohoku Imp. Univ. Sapporo, V, 1913.

<sup>3</sup> Jour. Coll. Agr. Tohoku Imp. Univ. Sapporo, VI, 1914.